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Batrachology as a distinct scientific discipline

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Although amphibians and reptiles have been considered as two distinct classes of vertebrates for more than 150 years, the study of both groups is still traditionally referred to a single scientific discipline, "herpetology". It is here argued that, both for scientific reasons and in order to have a better efficiency in the field of conservation, it is necessary to recognize two discrete scientific disciplines: "herpetology" for the study of reptiles and "batrachology" for that of amphibians. The first steps in the direction of this distinction already taken by some zoologists are outlined.

A general trend in science today is towards greater specialization. This has become more and more necessary as the amount of knowledge already accumulated and the bibliographical corpus have been growing, as techniques have been multiplying and becoming increasingly sophisticated, and as it has become impossible for any single scientist to master all problems, methods and results.

Whereas this trend is unavoidable, it also implies the risk that biologists might lose sight of the unity of biology. In order to minimize this risk, it is important that they both reach a high specialization in their own research work (a condition for efficiency of the latter) and keep a certain encyclopaedism of the mind and of general knowledge (a condition for being able to put their own research back in a more general context).

Zoology is one of the domains of biology where specialization of research and of knowledge has been growing progressively from the beginning. The specialization movement has developed in three major directions, which correspond to three major approaches to zoology.

(1) The first approach may be qualified of "systematic". Following the increasing subdivision of the animal kingdom into distinct groups, each of these became the object

of a particular sector of zoology, such as malacology for molluscs or entomology for insects. Each of these disciplines is centered on the animal group studied, on the peculiar characters separating it from related groups, on its internal diversity and variability, and on its history and evolution.

(2) In the second approach, the accent is not put on the animal groups themselves or on their peculiarities, but rather on the study of general structures, patterns and processes irrespective of the groups where they occur. Disciplines such as embryology (study of development) or ethology (study of behaviour), to take only two examples, tend to use the animals as a "material", devoid, in itself, of any particular interest, but allowing the discovery of (more or less) general laws. These disciplines are not alternative to those of the first kind, but rather *orthogonal* to them, since a behavioural study of a bird, for example, both belongs to the field of ethology and to that of ornithology.

(3) Finally, the important multiplication of zoological methodologies and the growing sophistication of many techniques has made necessary the development of "disciplines" such as histology or karyology, which do not correspond in fact to conceptual fields, but to technical ones. Although for practical reasons of information inflation these "disciplines" have their own specialists, teachings, journals, they lack specific problems and are only at the service of the disciplines of the first two categories.

Whereas disciplines of the second kind described above tend to be dominant in current zoology, it should be clear that those of the first one are to be firmly defended. They allow insights into the evolutionary biology of organisms and prevent zoology from becoming purely reductionist. This need is recognized by many zoologists. However, even acknowledgement of the need leaves the question of how many different "systematic" zoological disciplines should be distinguished. In this respect, there is the question rarely addressed until now, whether there should be a single zoological discipline, "herpetology", for both reptiles and amphibians, or two disciplines, "herpetology" for reptiles and "batrachology" for amphibians. In this paper I will address the justification of the latter distinction.

Amphibians and Reptiles

Amphibians and reptiles have not always been recognized as two distinct groups of the same hierarchical rank (class) within the taxinomic system.

Linné (1758) did not recognize these two groups as classes. He recognized a class Amphibia, with three orders, each of which contained several genera: Reptiles (*Testudo, Draco, Lacerta* and *Rana*), Serpentes (*Crotalus, Boa, Coluber, Anguis, Amphisbaena* and *Caecilia*) and Nantes (*Petromyzon, Raja, Squalus, Chimaera, Lophius* and *Acipenser*). In the light of our current knowledge, these orders and genera are highly heterogeneous, and the Amphibia of Linné are an assemblage of reptiles, amphibians and of various groups of "fishes". Later, Linné (1767) recognized a fourth order of Amphibia, Meantes, for the single species *Siren lacertina* (see Dubois, 1991).

Laurenti (1768) recognized a class Reptilium, with three orders: Salientia (*Pipa,*

Bufo, Rana, Hyla and part of *Proteus*[1]), Gradientia (part of *Proteus*[1], *Triton, Salamandra, Caudiverbera, Gekko, Chamaeleo, Iguana, Basiliscus, Draco, Cordylus, Crocodylus, Scincus, Stellio* and *Seps*) and Serpentia (*Chalcides, Caecilia, Amphisbaena, Anguis, Natrix, Cerastes, Coronella, Boa, Dipsas, Naja, Caudisona, Coluber, Vipera, Cobra, Aspis, Constrictor* and *Laticauda*). As can be seen from this list of genera, while his Salientia contained only amphibians, both his Gradientia and his Serpentia were a mixture of amphibians and reptiles.

It is only in 1799 when Alexandre BRONGNIART (in a paper first published, in two parts, in 1800; see DUBOIS, 1984: 10) presented to the French Academy of Sciences the first classification separating, at the ordinal level, the amphibians (under the name Batraciens) from the other "reptiles" (maintained in three distinct orders: Chéloniens, Sauriens and Ophidiens). BRONGNIART's Batraciens contained both the anurans and the urodelans, but not the gymnophiones (then all classified under the generic name *Caecilia*), which this author considered to be insufficiently known to be properly given a place in his system.

DUMÉRIL (1808: 317) was the first author to point to the high similarity of *Caecilia* with the batrachians, and his student OPPEL (1810: 409) was the first to clearly place this genus in the order Batracii, which he still considered part of the class Reptilia.

Another student of DUMÉRIL, [DUCROTAY] DE BLAINVILLE (1816 a-b, 1818), was the first author to give the amphibians (including *Caecilia*) and the reptiles the same rank in classification, since he considered these groups to be either two subclasses (Ornithoïdes and Ictyoïdes) of the class Reptiles, or two independent classes (Squammifères and Nudipellifères). He did not choose between these two possibilities in his 1816 a-b and 1818 works, but he did so in his 1822 book, where he was the first author to clearly recognize a class Reptiles and a class Amphibiens. MERREM (1820) also recognized these two classes, but under the names Pholidota and Batrachia (Amphibia s. str.). GRAY (1825), in a famous paper, also distinguished a class Reptilia and a class Amphibia (including *Caecilia*). Since then, except for a few exceptions in the early years, all authors have adopted this classification, which is still in use today, at least for living forms (some difficulties arise for assigning some fossil forms, but these need not be discussed here).

It is therefore more than 150 years since the amphibians and reptiles were last considered a single group of vertebrates. On the other hand, during the same period, the study of both kinds of animals has been referred to a single discipline of zoology, that of herpetology, and only recently has this been challenged. It is therefore justified to look for the reasons of this long period of stability.

1. LAURENTI's (1768) work provides an extraordinary example of non truly hierarchical classification, which has been overlooked by most authors until now: his genus *Proteus* straddles his two orders Salientia and Gradientia, with one species (*P. raninus*) in the former, and two (*P. tritonius, P. anguinus*) in the latter. The nomenclatural status of the generic name *Proteus* was only fixed by STEJNEGER's (1936) subsequent designation of *P. anguinus* as its type species, a fact which was ignored in FROST's (1985) checklist (see DUBOIS, 1987 b).

THE HISTORICAL REASONS FOR THE LONG MAINTENANCE OF HERPETOLOGY AS A SINGLE DISCIPLINE

In my opinion, the primary reason for the long maintenance of herpetology as a single discipline is to be found in both the relatively low number of species of amphibians and reptiles, and in the low level of interest long given, even by scientists themselves, to these animals. Furthermore, amphibians and reptiles are superficially very similar, which explains that they were first placed in a single group, and once a historical tradition has been well entrenched it is difficult to change.

In 1985, the number of recognized species was fewer than 3500 amphibians and 6000 reptiles (DUBOIS, 1988: 62), thus less than birds (more than 9000) and "fishes" (more than 21000), and only comparable to the number of known species of mammals (more than 4000). Besides, most species of amphibians and reptiles have little or no direct economic interest or value, in contrast to fishes, birds and mammals. Amphibians and reptiles have long been considered "inferior" vertebrates, of much less interest than mammals, which are "closer to man", "more evolved" and more useful for medical and other applied reasons.

As a result, the number of scientists studying amphibians and reptiles has long been very low, with few positions available in academic or private institutions for their study. In many museums, a single person is in charge of the collections of both groups (and sometimes also of others) and has to deal with scientific problems pertaining to both.

As a consequence of the few specialists working on amphibians and reptiles, the number of scientific publications dealing with these animals has remained relatively low as well, and the knowledge of these groups has lingered far behind that of the other groups of vertebrates. Furthermore, the (relatively) few specialists on these animals have tended to group themselves in learned societies devoted to the study of both groups, and which have started, one after another, the publication of scientific journals also dealing with both groups (and sometimes also of others). Whereas the groups amphibians and reptiles have clearly been considered distinct since the beginning of the XIXth century, the discipline "herpetology", dealing with both amphibians and reptiles, has become established as a "natural" discipline of zoology.

SOME TERMINOLOGICAL PROBLEMS

The name *herpetology* was coined by KLEIN (1755), under the form *herpetologia*, for the branch of zoology dedicated to the study of snakes and serpentiform animals. This term is derived from the Greek ἑρπετόν, meaning, according to the authors, either reptile or snake. It was used again by BONNATERRE (1789), under the form *erpétologie*, for the study of "snakes and reptiles" (the latter including the amphibians), by RAFINESQUE[-SCHMALTZ] (1814 a: 47, 1815: 39, *erpétologie*; 1814 b-c-d, *erpetologia*) and a few other authors of this period, but it became widely used only with the publication of DUMÉRIL &

BIBRON [& DUMÉRIL]'s *Erpétologie Générale* (1834-1854). The spelling starting with an *h*, which had first been introduced by KLEIN (1755) but had then been abandoned, was reintroduced by English-speaking authors such as HOLBROOK (1842), and has since then won general acceptance.

Although most authors until now have referred the study of both amphibians and reptiles to a single discipline "*herpetology*", there were some exceptions, even as far back as more than one century ago. For example, STEINDACHNER clearly distinguished between *herpetological* (STEINDACHNER, 1867, 1870, 1891, 1895, 1901 a-b, 1907) and *batrachological* studies (STEINDACHNER, 1864 a-b, 1882). The term *batrachology* is derived from the name *Batrachia*, a latinization (first used by ROSS & MACARTNEY, 1802: tabl. III) of the French name *Batraciens*, created by BRONGNIART (1800 a: 82) for the order including all recent amphibians. BRONGNIART (1800 a) may have based his new name either on the Latin name *Batrachi*, proposed by BATSCH (1788: 437) for a taxon of the rank family, or directly on the Greek name βάτραχος, meaning frog, which is also the root of BATSCH's name (see DUBOIS, 1984).

Another term, that of *amphibiology*, has been used incidentally by a few authors, both in the XIXth century (e.g. RAFINESQUE, 1840; BONAPARTE, 1845, 1850, 1852 a-b) and in the XXth century (e.g. TAYLOR, 1947). This name is based on the name *Amphibia*, derived from the Greek name ἀμφίβιος ("which lives in two elements, on the ground and in water"). The name *Amphibia* was the name given by LINNÉ to one of his classes of vertebrates, and which has been retained by the subsequent authors for the class containing the anurans, urodelans and gymnophiones.

DUBOIS (1984) proposed to stabilize the use of the names *Amphibia* and *Batrachia*, the first one being retained for the class as a whole, and the second one for the subclass including all living amphibians. For the latter, the name *Lissamphibia* (created by HAECKEL, 1866) has also been used by a few authors (following ROMER, 1966), but the name *Batrachia* has been used much more and is universally known, so that it should be retained (see DUBOIS, 1984). If this is done, the use of the term *batrachology* is warranted for all studies dealing with all amphibians belonging to the three living orders of the class Amphibia (not only anurans). The name *amphibiology*, on the other hand, would be the correct term for the field covering the study of all amphibians, including all fossil groups.

The creation of the journal *Alytes* in Paris in 1982 led to a wider usage of the terms *batrachology*, *batrachologist* and *batrachological*. This runs counter to the direction described above. Let us then examine the reasons for such a change.

THE NEED OF BATRACHOLOGY

The major reason for recognizing batrachology as a distinct discipline is not a simple demand for intellectual rigour and elegance, but the need of a better efficiency in research and conservation. Specialization permits a better communication among scientists studying these animals and among those interested in their conservation and in that of their environment.

Table I. — Number of papers dealing with the five major groups of Vertebrates listed in the *Zoological Record* from 1953 to 1987.

Year	Pisces	Amphibia	Reptilia	Aves	Mammalia
1953-57	5775	2777	3087	10903	8595
1958-62	8752	4719	4317	11309	11474
1963-67	10561	6493	5838	18728	25859
1968-72	22214	6720	6986	22514	30681
1973-77	24567	5092	8540	35338	27883
1978-82	32112	6110	12147	42542	36570
1983-87	38673	7397	12440	49314	46390

A first remark of some relevance is that the number of papers dealing with amphibians is much lower than those for the other four major groups of vertebrates (see Table I and fig. 1). However, relative progression of scientific research dealing with amphibians has been very strong in the recent years, similar to those for the other vertebrates (see Table II and fig. 2). The current increase in the number of species of amphibians described yearly in the world is still very strong: its curve is still far from reaching the plateau characteristic of such sigmoidal curves (Steyskal, 1965), which means that there remains, in amphibians, a very high number of species to describe and of systematic problems to solve (Dubois, 1977 b). The same is true in all other domains of the biology and evolution of these animals, where our knowledge is still very incomplete. Therefore amphibians, which have long been considered of little interest and importance, are attracting more and more attention. As such, their study should be highlighted by the recognition of a specific discipline devoted to it.

That living amphibians are monophyletic now seems to be admitted by all authors (Rage & Janvier, 1982; Milner, 1988). This group is relatively small and homogeneous, which makes it possible for a single researcher or team to have a rather complete and general approach of the knowledge accumulated on these animals in any given field of research (Dubois, 1977 b). Actually, comparative studies in various fields of research (morphology, anatomy, phylogeny, genetics, biochemistry, physiology, ethology, ecology, etc.), are much more effective, meaningful and instructive within a homogeneous group. But besides this set of reasons, which also apply to other "systematic" disciplines of biology as defined above, the recognition of batrachology as a discrete discipline is also strongly supported by other arguments, which rely on the unique properties of amphibians among vertebrates.

Amphibians share indeed many strange peculiarities lacking in other vertebrates and which make this group very special. Let us just stress some of them.

Amphibians, as their name indicates, usually go through a double life, with a larval stage separated from a post-larval stage by a metamorphosis. This has made the amphibians crucial for the study of development, which is true from the beginnings of embryology as a scientific discipline. From the XVIIIth century, embryologists have studied amphibian embryonal and larval development, and noted their peculiarities when contrasted with other vertebrates. Physiologists have long been interested in amphibian

Table II. — Relative increase in the number of papers dealing with the five major groups of Vertebrates listed in the *Zoological Record* from 1953 to 1987 (measured as the ratio to the number of papers listed for the period 1953-57, the latter being given the value 100). (Based on the data in Table I).

Year	Pisces	Amphibia	Reptilia	Aves	Mammalia
1958-62	152	170	140	104	133
1963-67	183	234	189	172	301
1968-72	385	242	226	206	357
1973-77	425	183	277	324	324
1978-82	556	220	393	390	425
1983-87	670	266	403	452	540

metamorphosis, which has no counterpart in other tetrapods, and in its anomalies (neoteny, paedogenesis, etc.).

Particularly relevant to the present discussion is the observation that, of the very large number of papers dealing with amphibian development and metamorphosis, and with various kinds of aneuchrony (DUBOIS, 1987 a) in these animals, published in this century, only a very few appeared in "herpetological" journals. The reason is simple to understand: for developmental biologists, there is little relevance in a "discipline" associating the amphibians with the reptiles. If embryologists were to associate the reptiles with another animal group, no doubt it would be the birds, and, if amphibians had by all means to be grouped with other animals, the least bad choice would be "fishes". This is certainly one of the reasons, although not the only one, why embryologists and physiologists have tended to publish their works on amphibian development in journals of general zoology, of experimental zoology or of developmental biology, rather than in "herpetological" ones (another reason for this is clearly the fact that developmental biologists tend to believe that they are studying general phenomena that cross major taxa). This tendency has been disastrous with respect to the synthetic appraisal of amphibian biology as a whole: most "herpetologists" who have dealt with the general features of amphibian biology have ignored, or grossly underexploited, the literature dealing with the biology of development of these animals.

It is very striking for example to realize that the classic and historical papers of embryologists of amphibians as important as F. BALTZER, E. BATAILLON, L. BOUNOURE, J. BRACHET, R. BRIGGS, A. DALCQ, G. FANKHAUSER, M. FISCHBERG, L. GALLIEN, E. HADORN, G. & O. HERTWIG, J. HOLTFRETER, R. R. HUMPHREY, T. J. KING, J. ROSTAND, W. ROUX, H. SPEMANN or E. WITSCHI do not appear in the bibliography of an important recent treatise on the biology of amphibians. Similarly, it cannot be denied that submission of papers dealing with the developmental biology of amphibians to traditional "herpetological" journals often leads to very feeble reviews, including irrelevant comments or suggestions. Many of the editors of such journals have few contacts with the world of developmental biology and little knowledge in this discipline. Developmental biology of amphibians is not only absent, or almost so, from "herpetological" journals, but also from "herpetological" meetings, congresses and courses.

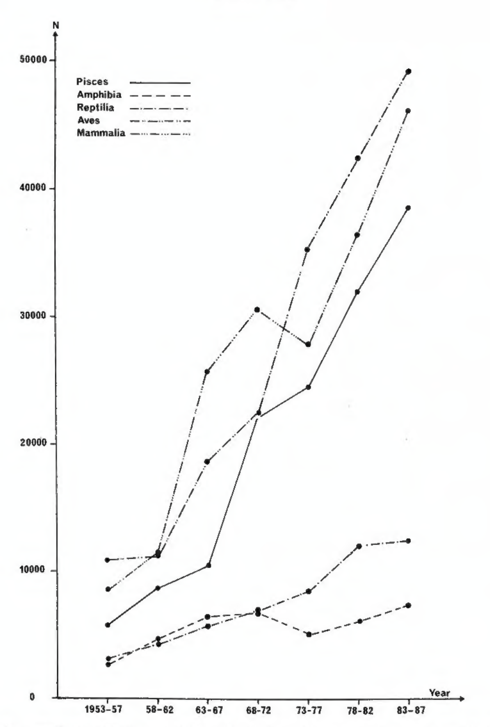


Fig. 1. — Number (N) of papers dealing with the five major groups of Vertebrates listed in the *Zoological Record* from 1953 to 1987. (From the data in Table I).

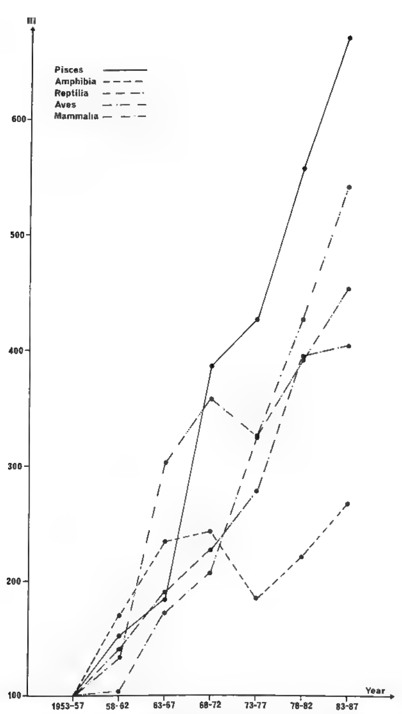


Fig. 2. Relative increase (RI) in the number of papers dealing with the five major groups of Vertebrates listed in the *Zoological Record* from 1953 to 1987 (measured as the ratio to the number of papers listed for the period 1953-57, the latter being given the value 100) (From the data in Table II).

If the biology of amphibians is to become a unified field, this situation must change drastically. The association, in a single journal, of papers dealing with the developmental biology of amphibians and of the other aspects of the biology of these animals, would certainly be extremely profitable to all amphibian biologists, whatever their specialization.

The existence of a larval stage in amphibians is not only interesting for embryologists. Amphibian larvae have long been ignored by biologists, both as animals in themselves and as parts of aquatic ecosystems. Recently however, more and more attention has been given to the fact that tadpoles are full organisms that have their own morphology, anatomy, physiology and behaviour, and that the two stages vital cycle of amphibians poses peculiar problems to the study of their ecology. Amphibian larvae represent an important fraction of the total animal biomass in some aquatic ecosystems, and play a significant rôle in the filtration of these waters, possibly comparable to that of earthworms in the ground. Until now, such factors have been underestimated by limnologists and other ecologists, possibly because tadpoles, being "only" larvae, tend rarely to be considered as significant components of ecosystems: in temperate countries (where many biologists live), tadpoles of a number of species only occur seasonally in aquatic ecosystems

The peculiarities of the life cycle and of the ecology of amphibians entail other consequences, especially as concerns the conservation of the populations and species of these animals. Because most species of amphibians breed in fresh water, the disappearance of lakes, ponds, marshes, torrents, streams, or their modification (through pollution or through other changes, usually caused by man: see e.g. Dubois, 1980), is usually a major threat to amphibians. Some of these facts have not been given the proper attention previously. For example, whereas the effects of the pollution of continental waters by acid rain and other sources are being more and more studied, little interest has been devoted to the effect of the recent important increase of the introduction of fishes into closed continental waters, particularly of salmonids into mountain lakes, on amphibian populations and species. Amphibians may also be threatened by other factors (collecting for consumption of frog legs, for teaching and research; modification and pollution of terrestrial, not only aquatic, ecosystems; introduction of alien species into ecosystems, and even displacement of amphibians, leading to genetic or faunistic pollution) (see e.g., Dubois, 1976, 1977 a, 1983a-b, 1985; Dubois & Morère, 1980). Altogether, the worldwide situation of amphibians is extremely worrying. It is more than time for specialists of these animals to assemble the information they have accumulated, and to work together to try and find solutions to the acute problems amphibians face, to propose actions and measures to governments and other organizations and agencies, and to see that these are carried out.

Consequently, recognition of batrachology as a discrete discipline, besides its purely scientific reasons, has the most important justification of greatly increasing the efficiency of their conservation. This aim is certainly worthwhile, indeed critical, if some amphibians are to survive into the next century.

FIRST STEPS TOWARDS THE RECOGNITION OF BATRACHOLOGY

The idea of the recognition of batrachology has been "in the air" for a long time, and I can remember having heard or supported it in conversations with colleagues more than 20 years ago. However, the first official act was the creation (in February 1982 at the Paris Museum) of *Alytes* as the first journal in the world to be specifically devoted to the biology of amphibians. This was followed in November 1982 by the foundation of the Société Batrachologique de France (S.B.F.), which accepted the task of publishing *Alytes*, and later, in November 1988, by the foundation of the International Society for the Study and Conservation of Amphibians (ISSCA), to which the journal was again transferred.

The statutory aims of ISSCA are "to contribute on a world scale:

– to the study and knowledge of amphibians (batrachology);

– to the conservation of amphibians and to that of their environment;

– to the establishment, reinforcement and facilitation of bonds among batrachologists;

– to the promotion of batrachology as an independent scientific discipline." (Article 2.1 of the Statutes of ISSCA).

However the recognition of batrachology as a distinct scientific discipline cannot be the work of a single society and a single journal. It will become a fact only if this idea is supported by multiple specialists of amphibians, as well as of specialists of reptiles. The use of the terms "batrachology" and "batrachologist" in the scientific literature, and, complementarily, that of the terms "herpetology" and "herpetologist" in a restrictive sense, referring only to the study of reptiles, will help achieve this recognition. Organization of meetings dealing only with batrachological or herpetological topics will also play a positive rôle in this direction.

Many biologists still are working on both groups of animals and, in all events, specialists on these two groups will continue to collaborate for many kinds of studies (particularly in the fields of ecology and faunistics). However, recognition of two distinct fields of research is likely to help rather than hinder this collaboration. It is also clear that the collaboration is likely to be fruitful between batrachologists and specialists of still other groups, in particular ichthyologists, limnologists, or all other biologists working on animal groups in which larvae and metamorphoses do occur: possibly, in the future, a new biological discipline, "larvology", could slowly emerge. But this is another story.

RÉSUMÉ

Bien que les Amphibiens et les Reptiles soient considérés comme deux classes distinctes de Vertébrés depuis plus de 150 ans, l'étude des deux groupes est encore traditionnellement rapportée à une seule discipline scientifique, l'"herpétologie". Il est ici suggéré qu'il est désormais nécessaire, à la fois pour des raisons scientifiques et pour

pouvoir avoir une meilleure efficacité dans le domaine de la conservation, de reconnaître deux disciplines scientifiques distinctes: l'"herpétologie" pour l'étude des Reptiles et la "batrachologie" pour celle des Amphibiens. Les premiers pas déjà effectués dans cette direction par certains zoologistes sont soulignés.

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Images d'Amphibiens camerounais. III. Le comportement de garde des œufs

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The eggs are guarded by one of the parents in six genera of Cameroonian Anurans. Seven photos illustrate this behaviour in the genera *Petropedetes, Alexteroon, Phrynodon, Nectophryne* and *Hemisus*. In several, if not all, cases, the hypothesis of a protection against predators does not seem to be acceptable.

Sur 39 genres d'Anoures représentés au Cameroun, 9 comprennent des espèces qui accordent des soins à leur descendance. Ceux-ci se ramènent à deux types de comportements parentaux : la surveillance des œufs et la construction de nids. Fait curieux, la batrachofaune camerounaise – et plus généralement africaine – montre un " vide éthologique " en ce qui concerne deux autres types de comportements plus ou moins fréquents ailleurs: le transport des œufs et/ou des larves et les soins accordés aux têtards.

Les photos des figures 1 à 7 montrent des exemples de la garde des œufs. Elles fourniront l'occasion d'une mise au point sur les 6 genres d'Anoures camerounais qui pratiquent ce comportement (le cas des constructeurs de nid sera examiné dans un autre article).

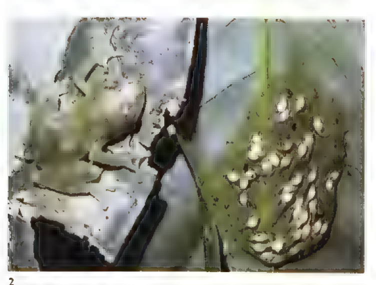
Le genre *Petropedetes*

La plupart des espèces de *Petropedetes*, comme l'indique leur nom générique, sont rupicoles, au moins en période de reproduction. Les œufs sont déposés en plaques, atteignant parfois une quinzaine de centimètres de plus grande dimension, sur des rochers recouverts d'un très mince film d'eau, plus rarement sur un support végétal, base de tronc d'arbre ou grande feuille. Les têtards, hygropétriques, broutent le revêtement de micro-organismes tapissant les rochers.

Chez *P. newtoni* (Bocage, 1895), *P. parkeri* Amiet, 1973, et *P. cameronensis* Reichenow, 1874 j'ai pu constater que, *la nuit*, il y a toujours, à proximité d'une plaque d'œufs, un mâle qui se tient immobile et qui, apparemment, en assure la garde (fig. 1: *P. newtoni*).



1

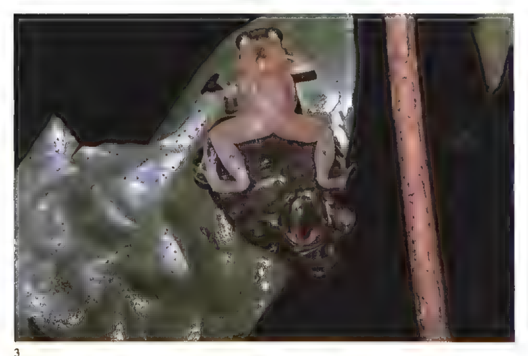


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Fig. 1. — Mâle de *Petropedes newtoni* (Bocage, 1895) à proximité d'une ponte (en haut de la photo). Kala, 22-I-79.

Fig. 2. — Cette femelle d'*Alexteroon obstetricans* (Ahl, 1931) a été trouvée à proximité de sa ponte et ramenée au laboratoire. En terrarium, elle est restée auprès de ses œufs, ou sur eux, jusqu'à la sortie des têtards. Ototomo, III-73.





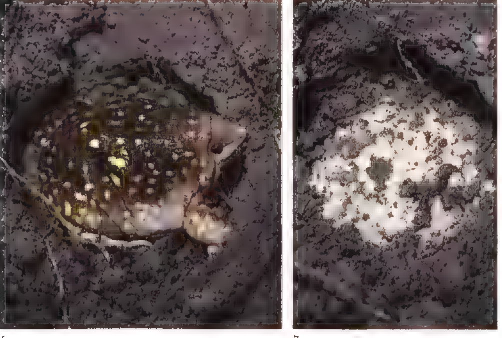
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Fig. 3. – Femelle de *Phrynodon sandersoni* Parker, 1935 sur sa ponte. A ce stade, les têtards, déjà munis de bourgeons de pattes postérieures, sont prêts à se libérer. Kala, X-70

Fig. 4. — Dans une cavité d'une grosse racine affleurant à la surface du sol, un mâle de *Nectophryne afra* Buchholz & Peters, 1875, appuyé sur ses membres antérieurs et aux deux tiers immergé, brasse l'eau où a été déposée la ponte. L'orifice du gîte était masqué par un morceau de bois tombé qui a été écarté fortuitement. Zamakoé, 27-IV-77

5



6 7

Fig. 5. Un couple d'*Hemisus guineensis* Cope, 1865 vient de se former après une journée de pluie dans les savanes d'Obala, au nord de Yaoundé. On remarquera que l'accouplement est lombaire, ce qui doit faciliter les déplacements du couple dans le sol où sera creusée la chambre de ponte. Obala, 3-III-72.

Fig. 6. Dans la paroi meuble d'un trou d'extraction de sable, un coup de pelle vient de mettre à jour une femelle d'*H. guineensis* sur sa ponte. Minkama, 6-III-78.

Fig. 7. Oeufs d'*Hemisus guineensis* dans la chambre de ponte, après enlèvement de la femelle. Minkama, 6-III-78.

Un mâle d'une autre espèce, *P. johnstoni* (Boulenger, 1887), dont les têtards sont probablement terrestres, a été observé près d'une ponte dans la matinée mais je ne peux pas dire si, chez les espèces précitées, les pontes sont surveillées aussi pendant la journée, car l'approche de l'observateur peut déclencher la fuite du mâle avant même qu'il ait pu être repéré.

Il est cependant probable que, chez les espèces rupicoles, les pontes ne soient gardées que la nuit.

LE GENRE *PHRYNODON*

Jusqu'ici, ce genre ne comprend qu'une seule espèce nommée, *P. sandersoni* Parker, 1935, répandue dans la plaine littorale ainsi que sur le versant et le rebord ouest du Plateau sud-camerounais, mais il existe aussi deux espèces orophiles non nommées sur les reliefs de la Dorsale camerounaise. *P. sandersoni* n'est pas rare dans les collines de la région de Yaoundé où il se localise dans les fonds de vallon en forêt de type primaire.

Dans un travail consacré à la biologie de cette espèce (AMIET, 1981), j'ai déjà relaté comment la femelle monte chaque soir sur sa ponte, déposée sur une feuille à quelques dizaines de centimètres (parfois jusqu'à 2 m) au-dessus de zones mouilleuses, et la "couve" jusqu'au lendemain matin.

Ce comportement se manifeste pendant toute la période de développement des œufs, soit une douzaine de jours. Les œufs, au nombre de 12 à 17, mesurent 2,3 mm de diamètre et sont disposés sur une seule couche. La gangue gélatineuse qui entoure chaque œuf est d'abord peu épaisse mais elle va gonfler progressivement, en même temps que s'élargit la cavité occupée par le jeune têtard. De ce fait, la ponte finit par ressembler à une masse mamelonnée atteignant 3 cm de plus grande dimension. L'attitude de la femelle est alors assez comique car, même en écartant largement ses membres, elle n'arrive plus à recouvrir complètement son encombrante progéniture (fig. 3).

Une femelle ne paraît pas capable de reconnaître sa propre ponte : elle peut, en captivité, accepter une autre ponte que la sienne, même si elle n'est pas au même stade de développement. En revanche, si on présente une ponte à une femelle non "incubante", elle s'en désintéresse.

LE GENRE *ALEXTEROON*

Chez *A. obstetricans* (Ahl, 1931), espèce placée auparavant dans le genre *Hyperolius*, les œufs sont pondus, au nombre d'une cinquantaine, sur une feuille surplombant le cours d'une petite rivière, à au moins 1,5 m de la surface de l'eau (AMIET, 1974).

Il est assez paradoxal que chez cette espèce peu commune, difficile à capturer, le

comportement de garde des œufs soit connu depuis près de 90 ans. BRANDES & SCHOENICHEN ont en effet publié en 1901 une photo (reproduite dans AHL, 1931) qui représente une femelle surveillant ses œufs déposés sur une feuille.

J'ai pu refaire cette observation et constater que la femelle se tient pendant la journée à proximité de sa ponte, sur laquelle elle se place durant la nuit. Je l'ai vue "ratisser" à l'aide de ses membres postérieurs la surface de la ponte: il est possible, mais non certain, que ce comportement ait pour effet d'aider les têtards à sortir de la gelée qui les entoure[1].

LE GENRE *NECTOPHRYNE*

La ponte et le développement de *N. afra* Buchholz & Peters, 1875 ont été décrits par SCHEEL (1970) J'ai pu refaire les mêmes observations sur cette espèce ainsi que sur *N. batesi* Boulenger, 1913 et découvrir de plus quels sites de ponte elles utilisent dans la nature.

Les *Nectophryne* pondent leurs œufs, réunis en cordon comme chez les autres Bufonidae mais entièrement blancs et assez volumineux, dans des petites cavités d'arbre contenant de l'eau. Ces cavités n'occupent pas toujours une situation élevée : celle qui a permis de réaliser la photo de la figure 4 se trouvait dans une racine affleurant à la surface du sol. Il est possible que d'autres "aquariums naturels" soient utilisés, en particulier les bases de pétiole de Macabo, où peut s'accumuler une quantité d'eau suffisante pour le développement des minuscules têtards de cette espèce, mais j'ai prospecté en vain ce type de biotope. En revanche, on m'a apporté une ponte trouvée dans une boîte de conserve abandonnée sur le sol où s'était accumulé un peu d'eau !

La surveillance des œufs est assurée par le mâle. Comme l'a montré SCHEEL (1970), la garde est permanente et, de plus, le mâle, en s'appuyant sur ses mains aux parois de la cavité, "pédale" dans l'eau avec ses pattes postérieures, ce qui a probablement pour effet d'aérer la ponte.

LE GENRE *TRICHOBATRACHUS*

PERRET (1966) rapporte qu'il a trouvé un mâle de grenouille poilue, *T. robustus* Boulenger, 1900, "immergé à environ 60 cm de profondeur sous un fort courant d'eau dans un trou rocheux alors qu'il semblait protéger une masse d'œufs avec des embryons déjà bien avancés".

1 Le nom donné par AHL (1931) à cette espèce doit s'inspirer d'une observation similaire rapportée par BRANDES & SCHOENICHEN (1901), dont je n'ai pas eu l'article en mains et que je cite ici d'après PERRET (1988) Ce dernier precise d'autre part que le nom générique *Alexteroon*, dont il est l'auteur, est dérivé du grec "alexter" = protecteur et "oon" = œuf Peu d'especes doivent avoir un nom générique et un nom spécifique faisant allusion à une particularité comportementale..

Le genre *Hemisus*

Remarquablement adapté à la vie fouisseuse, ce genre est représenté au Cameroun par deux espèces savanicoles, *H. marmoratus sudanensis* Steindachner, 1863 et *H. guineensis* Cope, 1865. Grâce à Wager (1965), on sait que les *Hemisus* pondent leurs œufs dans une chambre creusée dans la berge d'une mare et que la femelle reste sur sa ponte. Les têtards, après l'éclosion, rejoignent le milieu aquatique grâce à une galerie de sortie forée par leur mère.

J'ai eu la chance de pouvoir observer une femelle d'*H. guineensis* juchée sur ses œufs, dans une cavité de la grosseur du poing à peu près, creusée dans la paroi d'un trou d'extraction de sable Les clichés des figures 5 à 7 montrent cette femelle photographiée juste après que la chambre de ponte eût été éventrée (fig. 6), ainsi que la masse d'œufs sur laquelle elle était installée (fig. 7).

Il est difficile de se représenter comment la chambre de ponte est creusée car la femelle, nécessairement, n'y arrive pas seule mais portant un mâle solidement agrippé à son arrière-train (l'accouplement se fait en effet à la surface du sol, comme le montre la photo 5) D'autres points restent à élucider · le mâle, après l'accouplement, quitte-t-il la chambre de ponte par la galerie empruntée auparavant par le couple ou en fore-t-il une autre? La voie suivie par les têtards n'est-elle pas la galerie de sortie du mâle plutôt qu'une galerie creusée par la femelle?

Discussion

Dans ce qui précède, les termes de "garde" ou de "surveillance" des œufs ont été utilisés faute de mieux. Ils ont l'inconvénient de laisser supposer que le parent concerné puisse exercer une protection de la ponte contre d'éventuels prédateurs ou agresseurs. Cette fonction, en fait, est très improbable pour les raisons suivantes

– Bien que Duellman & Trueb (1986) mentionnent divers animaux susceptibles de se nourrir de pontes d'Anoures (Opilions, Araignées, Crabes et Serpents) je n'ai pu déceler jusqu'ici de cas semblables au Cameroun, où j'ai pourtant effectué près de 1 200 sorties de nuit[2].

– Même si de tels prédateurs existent, on ne voit pas comment de petits Batraciens, eux-mêmes sans défense, pourraient protéger efficacement leur ponte contre un agresseur. Chez *Phrynodon*, et probablement *Petropedetes*, les pontes restent d'ailleurs abandonnées à elles-mêmes pendant la journée.

– Beaucoup d'autres Anoures de la faune camerounaise ont des pontes aériennes très apparentes ("pontes suspendues") auxquelles ils n'assurent aucune protection.

– La femelle, en se plaçant sur ses œufs comme elle le fait chez *Phrynodon* et *Alexteroon*, doit attirer l'attention des prédateurs mieux que ne le fait la ponte seule

En fait, la présence d'un des parents sur ou à proximité de la ponte peut avoir une fonction tout autre que la protection.

2 Au Gabon, les pontes aériennes de *Chiromantis rufescens*, déposées dans une masse d'écume battue, peuvent être pillées par un petit oiseau, *Nigrita bicolor*, ainsi que l'a montré Brosset (1976) Cela se produit aussi au Cameroun, mais très rarement

– Chez *Phrynodon*, le rôle de la femelle semble être d'humecter les œufs, non pas pour les protéger de la dessiccation, peu à craindre là où vit l'espèce, mais pour entraîner le gonflement de la gangue gélatineuse qui les entoure. J'ai constaté en effet (AMIET, 1981) que, en l'absence de femelle, les pontes fraîchement déposées montrent un début de développement des œufs mais que leur gangue reste mince: les embryons, comprimés dans leur enveloppe, dépérissent alors. Les pontes récoltées dans la nature à un stade plus avancé de gonflement ont une évolution normale, même en l'absence de femelle.

– En brassant l'eau avec ses pattes postérieures, le mâle de *Nectophryne* contribue probablement à aérer la ponte. Même si ce comportement a en réalité une autre fonction, il est difficile d'imaginer qu'il soit destiné à éloigner d'éventuels agresseurs.

– La présence de la femelle *Hemisus* dans la chambre de ponte (en elle-même protection efficace contre les prédateurs) peut s'expliquer par la nécessité de forer une voie d'accès à l'eau pour les têtards.

Ainsi, l'humectation des œufs chez *Phrynodon*, leur aération chez *Nectophryne*, le forage de la galerie de sortie chez *Hemisus* suffisent à justifier la présence d'un des parents. La question reste posée pour les *Petropedetes*, *Alexteroon* et *Trichobatrachus* mais, là encore, une fonction de protection contre les prédateurs semble peu plausible.

Résumé

La ponte est gardée par l'un des parents dans six genres d'Anoures camerounais Sept photos illustrent ce comportement chez les genres *Petropedetes*, *Alexteroon*, *Phrynodon*, *Nectophryne* et *Hemisus*. Dans plusieurs cas, sinon dans tous, l'hypothèse d'une protection contre les prédateurs ne paraît pas pouvoir être retenue.

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Faunal deficit of anurans in tropical farmland of Amazonian Peru

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Fifty-eight (= 89.2 %) of 65 identified anuran species at Panguana, a study site in the upper Amazon Basin in east-central Peru, occur in primary rainforest, 35 (= 53.9 %) in secondary forest, 21 (= 32.3 %) at the forest edge, 8 (= 12.3 %) at the margin of the Río Llullapichis, and 9 species (= 13.8 %) in farmland. The diversity of anuran reproduction in forest habitats was 2.3 times higher than in areas under cultivation. The faunal impoverishment of 84.5 % in relation to the number of species living in primary forest is caused by unfavorable environmental conditions, by the absence of appropriate habitats, and by changes in diet supply.

INTRODUCTION

In the humid environments of tropical rainforests, anurans have developed a great diversity of reproductive modes (DUELLMAN, 1988, HÖDL, 1990) Because of the different environmental conditions it seems reasonable to compare forest and non-forest habitats with respect to species composition and reproduction.

A study area at the lower Río Llullapichis in the upper Amazon Basin in east-central Peru disposed the required characteristics: (1) an area of about 2 km^2 mainly covered with unexploited primary forest and (2) adjacent areas under cultivation. The Panguana site (fig. 1b) was founded in 1968 by H.-W. KOEPCKE (Hamburg). Between 1959 and 1984 the areas under cultivation rapidly increased (compare fig 1a, b). Within a few years the rainforest plot of Panguana will be surrounded by farmland if rainforest destruction continues at the present rate.

Seventy-three anuran species occur at Panguana (DUELLMAN & TOFT, 1979; SCHLÜTER, 1979, 1981, 1984; HÖDL 1990; personal observations). Eight species of the genus *Eleutherodactylus* are still unidentified. According to the classification system of DUELLMAN & TRUEB (1986), the 65 identified species show 8 of 29 described reproductive modes: (mode 1) eggs deposited in open water with feeding tadpoles (25 species); (mode 3) eggs and early larval stages in constructed basins, subsequent to flooding feeding tadpoles in streams (*Hyla boans*); (mode 4) eggs and feeding tadpoles in water in tree holes (*Phrynohyas resinifictrix*, supposed for *Osteocephalus leprieurii*); (mode 14) eggs on ground, feeding tadpoles are carried by adult to water (7 species); (mode 17) eggs deposited out of water with direct development (13 species, 8 species unidentified, supposed for *Ischno-*

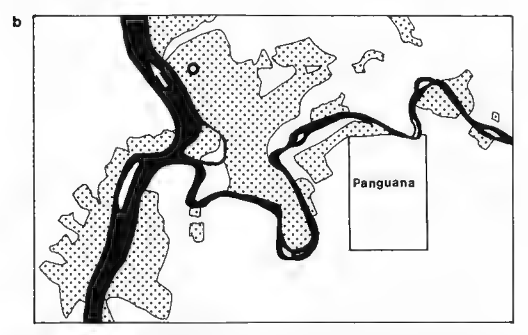


Fig. 1. – Distribution of farmland at the mouth of the Rio Llullapichis in 1958 (a) and 1984 and location of Panguana (b). Stippled areas: under cultivation. The circle in b marks the investigated farmland pond site. (Drawn after photographs taken by the Peruvian air-force in June 1958 and August 1984). The course of the river and the situation of islands changed between 1958 and 1984

cnema quixensis); (mode 18) eggs on vegetation above water, eggs hatching into tadpoles that drop into water (8 species, supposed for *Hyla rossalleni*); (mode 21) eggs in foam nests in burrows, subsequent to flooding, feeding tadpoles in ponds or streams (6 species); (mode 22) eggs in foam nests on land, non feeding tadpoles complete development in nest (2 species).

Because many anuran species with a variety of reproductive modes occur in such a small area in tropical rainforest it seems especially interesting to know: (1) how many and which species inhabit the different habitats; (2) if species do exist that are restricted to open areas; and (3) which reproductive modes are favoured by the environmental conditions in farmland.

Description of study site

Panguana is located on the south bank of the lower Río Llullapichis, a tributary of the Río Pachitea, in the upper Amazon Basin, 9°37′ S, 74°56′ W, at an elevation of 260 m (fig 1b). From November 1981 through October 1982, the total annual precipitation was 2635 mm. The rainfall is seasonal, with a marked dry period lasting from mid-March to mid-September (AICHINGER, 1987). On sunny days, daily maximum temperatures were about 6°C higher in farmland than in primary forest. Minimum relative humidity was between 35-40 % in farmland whereas it was seldom below 90 % in the forest (HANAGARTH, 1981).

The investigation area of Panguana is mainly covered with unexploited primary forest. Vegetation at sites of abandoned cultivated areas (compare fig. 1a, b), along a temporary stream, at the border of the Río Llullapichis, and at the forest edge are assigned to secondary forest. The edge of the forest is characterized by dense vegetation near ground level. The settlers around Panguana gain farmland by clearing primary forest. After burning the areas are planted with maize and subsequently with grass for cattle-breeding.

The two investigated ponds are situated about 2.8 km northwest of Panguana near the Río Pachitea in farmland belonging to Elvío MÓDENA (fig. 1b). The rainforest in this area was cleared in the late fifties; since then it has been used for cattle-breeding. The two ponds are surrounded by a dense vegetation of high grass and low "Niejilla" palm trees (*Bactris* sp.). They are about 300 m away from primary forest. Their maximum diameter was reached in January and measured about 8 m.

Methods

The study on annual activity patterns of anurans at Panguana, lasting from November 1, 1981 until October 31, 1982 (AICHINGER, 1987), included observations at two farmland ponds. I compare the anuran fauna of 4 different forest habitats (primary forest, secondary forest, forest edge, border of the Río Llullapichis) with that of the farmland.

In primary and secondary rainforest I investigated the anuran fauna in six plots of 100 m^2 each which were established at different aquatic sites (AICHINGER, 1987). The temporary pond at the forest edge had about the same size as the two farmland ponds (maximum diameter about 8 m). The border of the Río Llullapichis was observed along the limit of the study area. The course of the river and subsequently the situation of islands changed between 1958 and 1984 (compare fig. 1a, b).

Species are treated according to their reproductive modes. According to the number of ovarian eggs, coloration, and egg diameter (AICHINGER, 1985), the reproductive modes of *Ischnocnema quixensis* and *Hyla rossalleni* are preliminarily assigned. No observations on the egg-deposition site of *O. leprieurii* could be made. This large hylid frog calls dispersed in primary forest and did not aggregate at aquatic sites. I assume that this species, like *Phrynohyas resinifictrix*, deposits its eggs in water-filled tree holes (HÖDL, in press; ZIMMERMANN & HÖDL, 1983). *Dendrophryniscus minutus*, which lays strings of eggs on low vegetation up to 50 cm above water level, is assigned to mode 14.

Data for uncommon species observed only a few times or not at all during the course of this study are supplemented by CRUMP (1974), DUELLMAN (1978), TOFT & DUELLMAN (1979), and SCHLÜTER (1984).

RESULTS

The habitat distribution of 65 anuran species is given in Table I. Fifty-eight species (= 89.2 %) inhabited the primary forest. Twenty-seven species (= 41.5 %) were restricted to it. Twenty-nine species living in primary forest also occurred in secondary forest, which provided a habitat for 35 (= 53. 8 %) species. At the forest edge I found 21 species (= 32.3 %) at a temporary pond (AICHINGER, 1985, 1987): all also occurred in secondary forest, 17 in primary forest. Eight species (= 10.8 %) were found at the Rio Llullapichis. *Bufo marinus*, *B. typhonius*, and *Hyla boans* called during the dry season along the Río Llullapichis. In mid-September (early in the 6 month rainy season), *Leptodactylus pentadactylus* called at the river bank where no other anurans were found throughout the whole rainy season.

Nine species (= 13.8 %) occur at the two farmland ponds. They belong to the families Hylidae (8 species) and Leptodactylidae (1 species). I observed frogs only in the dense vegetation surrounding these ponds. No anurans were found in the pasture. Eight of the farmland species were also common in secondary forest. *Phyllomedusa tarsius* was observed in primary forest too. *Ololygon rubra* also occurred in the palm-leave roofs of native huts. *Bufo marinus*, most common near houses, hunting after insects attracted to artificial light, called at the river's edge and was not observed in farmland

The distribution of the reproductive modes of 65 anuran species at 5 habitats is shown in Table II. I included only species which were actually breeding (calling males and/or gravid females). Thus 3 species observed at the river edge (*Adenomera hylaedactyla*, *Bufo glaberrimus*, *Leptodactylus wagneri*) were excluded. Species occurring in primary forest used 7 modes of reproduction. Poison-dart frogs (mode 14) and species of the genus *Eleutherodactylus* (mode 17) occurred predominantly in primary forest. The number of

species with oviposition in water increased in secondary forest. Fourteen (= 66.7 %) out of 21 species found at the forest edge laid their eggs in water (mode 1). At the border of the Río Llullapichis, 60 % of the species underwent complete aquatic development.

The 9 species found at the two farmland ponds showed 3 reproductive modes. Five species (= 55.6 %) represent mode 1 Two species laid their eggs on vegetation above water (*Hyla leucophyllata, Phyllomedusa tarsius*). Arboreal oviposition is also supposed for *H. rossalleni*. The foam-nest producing *Leptodactylus wagneri* (mode 21) was heard calling at these aquatic sites. In farmland no species of poison-dart frogs (mode 14) or of the genus *Eleutherodactylus* (mode 17) occurred.

DISCUSSION

Of 65 anuran species known from Panguana, only 9 species (13.8 %) were found at the two farmland ponds. Only habitat generalists breed at these aquatic sites. No anuran species occurs exclusively in areas under cultivation. This faunal impoverishment seems to be due to changes in microclimate, habitat diversity, and food supply.

Microclimatic conditions in farmland favor only few amphibians. In open areas, high maximum temperatures correlated with low humidity restrict the occurrence of amphibians. Due to intensive sun irradiation, maximum temperatures are higher and humidity is lower in farmland than in forest habitats (HANAGARTH, 1981). The danger of desiccation forces the anurans living in farmland to hide during daytime in shady shelter sites. During night hours, when temperatures and humidity of rainforest and farmland are nearly equal (HANAGARTH, 1981), anurans become active. All species breeding in open areas are nocturnal (HEYER, 1976). The closed canopy of primary rainforest reduces sun irradiation and maintains high humidity; this is important for all anurans, especially those with terrestrial development.

Species with egg deposition directly in water (with subsequent development occurring there as well) represent the primitive mode of reproduction (DUELLMAN & TRUEB, 1986) These species are less dependent on the high humidity provided by a forest than those depositing eggs in terrestrial environments where all needed water is extracted from the air (LYNCH, 1979). Environmental conditions in farmland favor species depositing many eggs in open water. Reproductive generalists with high fecundity are better adapted for unpredictable environments (DUELLMAN, 1978). The mean egg number of the 5 aquatic breeding farmland species examined by AICHINGER (1985) ranged between 394 (*Hyla riveroi*) and 1170 (*Ololygon rubra*) (n = 10 − 15).

Four species at the farmland ponds do not deposit their eggs directly in the water. The species were less abundant than aquatic breeders. Two species lay their eggs on vegetation above water. This mode is also assumed for *Hyla rossalleni*. Development is endangered by a possible desiccation of eggs. *Phyllomedusa tarsius* encloses the egg mass with leaves. The top and the bottom of the clutch consist mainly of eggless capsules providing protection from sun irradiation (CRUMP, 1974). *Hyla leucophyllata* lays its eggs on leaves on low vegetation (up to a height of 50 cm), where humidity from the evaporating water surface may prevent desiccation. *Leptodactylus wagneri* reflects the primitive *Leptodactylus*

Table I. Distribution of 65 anuran species in 5 different habitats. PF = primary forest, SF = secondary forest, FE = forest edge, RE = river edge, FL = farmland. Categories correspond to reproductive mode numbers according to DUELLMAN & TRUEB (1986), * indicates species where data are supplemented by CRUMP (1974), DUELLMAN (1978), TOFT & DUELLMAN (1979), and SCHLÜTER (1984)

SPECIES	PF	PF only	SF	FE	RE	FL ponds
LEPTODACTYLIDAE						
1. *Adenomera andreae*	22	22				
2. *A. hylaedactyla*			22	22	22	
3. *Ceratophrys cornuta*	1		1	1		
4. *Edalorhina perezi*	21	21				
* 5. *Eleutherodactylus acuminatus*	17		17			
6. *E. altamazonicus*	17	17				
7. *E. carvalhoi*	17	17				
* 8. *E. diadematus*	17		17			
* 9. *E. imitatrix*	17	17				
10. *E. lacrimosus*	17	17				
* 11. *E. mendax*	17	17				
12. *E. ockendeni*	17	17				
13. *E. peruvianus*	17	17				
14. *E. sulcatus*	17	17				
15. *E. toftae*	17	17				
16. *E. ventrimarmoratus*	17	17				
17. *Ischnocnema quixensis*	17		17			
18. *Leptodactylus pentadactylus*	21		21	21	21	
19. *L. rhodomystax*	21		21			
20. *L. wagneri*	21		21	21	21	21
21. *Lithodytes lineatus*	21		21			
22. *Physalaemus petersi*	21	21				
BUFONIDAE						
23. *Bufo glaberrimus*			1		1	
24. *B. marinus*			1		1	
25. *B. typhonius*	1				1	
26. *Dendrophryniscus minutus*	18	18				
DENDROBATIDAE						
27. *Colostethus marchesianus*	14	14				
* 28. *C. peruvianus*	14	14				
29. *Dendrobates quinquevittatus*	14	14				
30. *Epipedobates femoralis*	14	14				
31. *E. petersi*	14	14				
32. *E. pictus*	14	14				
33. *E. trivittatus*	14	14				

HYLIDAE						
34. *Hyla boans*			3		3	
35. *H. brevifrons*	18		18	18		
* 36. *H. calcarata*	1	1				
37. *H. fasciata*	1		1	1		
38. *H. geographica*	1		1			
39. *H. granosa*	1		1	1	1	1
40. *H. leucophyllata*			18	18		18
41. *H. marmorata*			1	1		
42. *H. minuta*	1	1				
43. *H. parviceps*	1		1	1		
44. *H. rhodopepla*	1		1	1		
45. *H. riveroi*	1		1	1		1
46. *H. rossalleni*	18		18			18
47. *H. sarayacuensis*	18		18	18		
48. *Ololygon cruentomma*	1		1	1		1
49. *O. funerea*	1					
50. *O. garbei*			1	1		1
51. *O. rubra*	1		1	1		1
52. *Osteocephalus leprieurii*	4		4			
53. *O. taurinus*	1		1	1		
54. *Phrynohyas coriacea*	1		1			
* 55. *P. resinifictrix*	4	4				
56. *P. venulosa*	1		1			
* 57. *Phyllomedusa palliata*	18	18				
58. *P. tarsius*	18					18
59. *P. tomopterna*	18	18				
60. *P. vaillanti*	18		18	18		
CENTROLENIDAE						
61. *Centrolenella midas*	18		18			
62. *C. munozorum*	18	18				
MICROHYLIDAE						
63 *Chiasmocleis ventrimaculata*	1		1	1		
64 *Ctenophryne geayi*	1		1	1		
65. *Hamptophryne boliviana*	1		1	1		

Table II — Distribution of reproductive modes (after DUELLMAN & TRUEB, 1986) in 5 different habitats.

Reproductive mode	Total number of species	Primary forest	Primary forest only	Secondary forest	Forest-edge	River-edge	Farmland ponds
1	23 35.4 %	21 36.2 %	4 15.4 %	19 50.0 %	14 66.7 %	3 60.0 %	5 55.6 %
3	1 1.5 %			1 2.6 %		1 20.0 %	
4	2 3.1 %	2 3.4 %	1 3.8 %	1 2.6 %			
14	7 10.8 %	7 12.1 %	7 26.9 %				
17	13 20.0 %	13 22.4 %	9 34.6 %	3 7.9 %			
18	11 16.9 %	8 13.8 %	3 11.5 %	6 15.8 %	4 19.0 %		3 33.3 %
21	6 9.2 %	6 10.3 %	2 7.7 %	4 10.5 %	2 9.5 %	1 20.0 %	1 11.1 %
22	2 3.1 %	1 1.7 %	1 3.8 %	1 2.6 %	1 4.8 %		
Total	65 100.0 %	58 89.2 %	27 41.5 %	35 53.8 %	21 32.3 %	5 7.7 %	9 13.8 %

pattern (HEYER, 1969) in that a foam nest is placed on top of the water. Eight gravid females of *L. wagneri* examined by AICHINGER (1985) contained a mean number of 1726 eggs.

Tropical rainforests provide a great diversity of habitats. Anurans are well adapted to live in leaf litter, bushes, or in the forest canopy. At Panguana no anuran species with terrestrial breeding (Dendrobatidae, *Eleutherodactylus* spp., *Adenomera hylaedactyla*) occurs in farmland. These species require leaf litter as oviposition and shelter sites. All are restricted to forest habitats where leaf litter is abundant and humidity high throughout the day. Many anurans, especially hylid frogs, are adapted to the dense vegetation of bushes. In farmland this microhabitat was found only around the two investigated ponds. In forest habitats, 40 anuran species were found in bushes, whereas in farmland only 8 species occurred in this microhabitat. Even the species diversity of birds was remarkably higher in undisturbed primary forest than in cacao or coffee plantations (TERBORGH & WESKE, 1969). In California, logging of redwood forest opened the forest canopy and apparently favored only a few amphibian species to the detriment of the majority — the forest-dependent species (BURY, 1983).

Farmland habitats favor only broad-niched species. *Leptodactylus wagneri* is well adapted to changing environments and probably an excellent colonizer species (HEYER & BELIN, 1973). This seems also to be true for *Ololygon rubra*, which was found especially at ephemeral watersites.

Diet supply for food specialists, such as certain leaf-litter frogs (TOFT, 1980), may limit the existence in farmland. There, compared with primary forest, abundances of ants and termites are remarkably reduced; beetles, grasshoppers and crickets, however, are more abundant (HANAGARTH, 1981). The ant fauna is nearly completely destroyed by the cutting and burning of forests (VERHAAGH, in press).

Rainforest destruction leads to a reduction in the numbers of individuals of those species bound to primary rainforest (JACOBS, 1988). At Panguana environmental

conditions, shortage of food supply, and a remarkable deficit of habitat types in farmland result in a faunal impoverishment of 84.5 % compared with the anuran species living in primary forest.

RESUMEN

58 especies de batracios (= 89,2 %) de 65 especies identificadas de Panguana, una estacion de estudios en la parte alta de la cuenca amazónica central, ocurren en el bosque primario, 35 (= 53,9 %) en el bosque secundario, 21 (= 32,3 %) en el borde del bosque, 8 (= 12,3 %) en la orilla del Río Llullapichis y 9 especies (= 13,8 %) en los campos cultivados. La diversidad de reproducción de los batracios en los habitates selváticos fue 2,3 veces más alto que en los campos cultivados. El empobrecimiento faunístico de 84,5 % en relación al número de especies que viven en el bosque primario es posiblemente causado por las condiciones desfavorables del ambiente, la ausencia de habitates apropriados y los cambios de la provisión alimenticia.

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The title should be followed by the name(s) and address(es) of the author(s). The text should be organized as follows: English abstract, introduction, method, results, discussion, conclusion, French or Spanish abstract, acknowledgements, literature cited.

Figures and tables should be mentioned in the text as follows: fig. 4 or Table IV. Figures should not exceed 16 × 24 cm. The size of the lettering should ensure its legibility after reduction. The legends of figures and tables should be assembled on a separate sheet. Each figure should be numbered using a pencil.

References in the text are to be written in capital letters (SOMEONE, 1989; EVERYBODY et al., 1980; SO & SO, 1987). References in the literature cited section should be presented as follows:

– when in a periodical:

INGER, R. F., VORIS, H. K. & VORIS, H. H., 1974. – Genetic variation and population ecology of some Southeast Asian frogs of the genera *Bufo* and *Rana*. *Biochem. Genet.*, **12**: 121-145.

– when in a multi-authors book:

GRAF, J.-D. & POLLS PELAZ, M., 1989. – Evolutionary genetics of the *Rana esculenta* complex. *In*: R. M. DAWLEY & J. P. BOGART (eds.), *Evolution and ecology of unisexual vertebrates*, Albany, The New York State Museum: 289-302.

– when a book:

BOURRET, R., 1942. – *Les Batraciens de l'Indochine*. Hanoï, Institut Océanographique de l'Indochine: i-x + 1-547, pl. I-IV.

Manuscripts should be submitted *in triplicate* to Alain DUBOIS (address above) if dealing with amphibian morphology, systematics, biogeography, evolution, genetics or developmental biology, or to Günter GOLLMANN (address above) if dealing with amphibian population genetics, ecology, ethology or life history.

Acceptance for publication will be decided by the editors following review by at least two referees.

No page charges are requested from author(s), but the publication of color photographs is charged. For each published paper, 25 free reprints are offered by *Alytes* to the author(s). Additional reprints may be purchased.

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